

As indicated in Table I, Part I, the mean water temperature for April is 54.7° F. and that for November, 55.9° F. Thus, 55° F. is adopted as a critical temperature for Acmaea persona.

It is important to note that, despite Runnstrom's (1927) demonstration that adults are less sensitive to temperature than larval forms, it is the adult sensitivity which determines the reproductive period of Acmaea persona, since the gonads are completely nonfunctional during the summer months. Thus, although the larvae may be very sensitive to temperatures in excess of 55° F. or thereabouts, it is never a question of their susceptibility to temperature that determines the southern limit of the range since no larvae are produced above 55° F. If this is taken as the maximum at which A. persona spawns and this value is compared with the species range on the isocryme plate, it is seen that the southern range is terminated at the 55° isocryme. Acmaea persona, then, appears to be restricted in its southern distribution by the maximum temperature at which reproduction is possible, this being a function of the adult physiology.

Acmaea fenestrata cribraria Carpenter, 1857

Geographic range: Coal Harbor, Unga Island, Alaska, to Cayucos, San Luis Obispo County, California.

Latitudinal range: 60° - 35.5° N. Lat.

Isothere range: 50° - 60° F. (10°)

Isocryme range: 35° - 56.5° F. (21.5°)

As was the case with Acmaea persona, the period of reproductive activity of this species can be correlated directly with its northern distribution. Plate 16, Part II, shows that reproductively active animals are found only from September through April and during the summer the population is either spawned or sexually indeterminate. The upswing in August and September represents partially ripe animals, fully ripe forms not appearing until October and November. This pattern of activity does not bear close relation to sea temperatures prevailing during the assumed critical months of April and August, 54.7° and 59.8° respectively. However this may be, the redevelopment of the gonads begins during the period of the maximum yearly temperature, at least two months prior to that seen in A. persona. This difference may result from the different intertidal positions of the two species, since A. fenestrata cribraria occurs only in zone two and lower while A. persona is strictly a zone one animal facing slightly increased heating and desiccation. Or the reproductive difference between the two species may reflect the somewhat

greater warm water tolerance of A. f. cribraria. Unlike A. persona, a correlation between the maximum temperature at which spawning occurs and the distribution of the subspecies in relation to isocrymes cannot be made. The data indicate that 54° F. must be about the maximum spawning temperature for A. f. cribraria at the latitude of study. Yet, as shown on Plate 32, its range extends almost to the 57° isocryme producing a discrepancy of 3° F. It appears, nevertheless, that this subspecies is restricted in its southern distribution by the maximal temperature at which the adult reproductive mechanism can operate.

Acmaea scutum Eschscholtz, 1833

Geographic range: Aleutian Islands to San Pedro, California

Latitudinal range: 60° - 34° N. Lat.

Isothere range: 50° - 65.5° F. (15.5°)

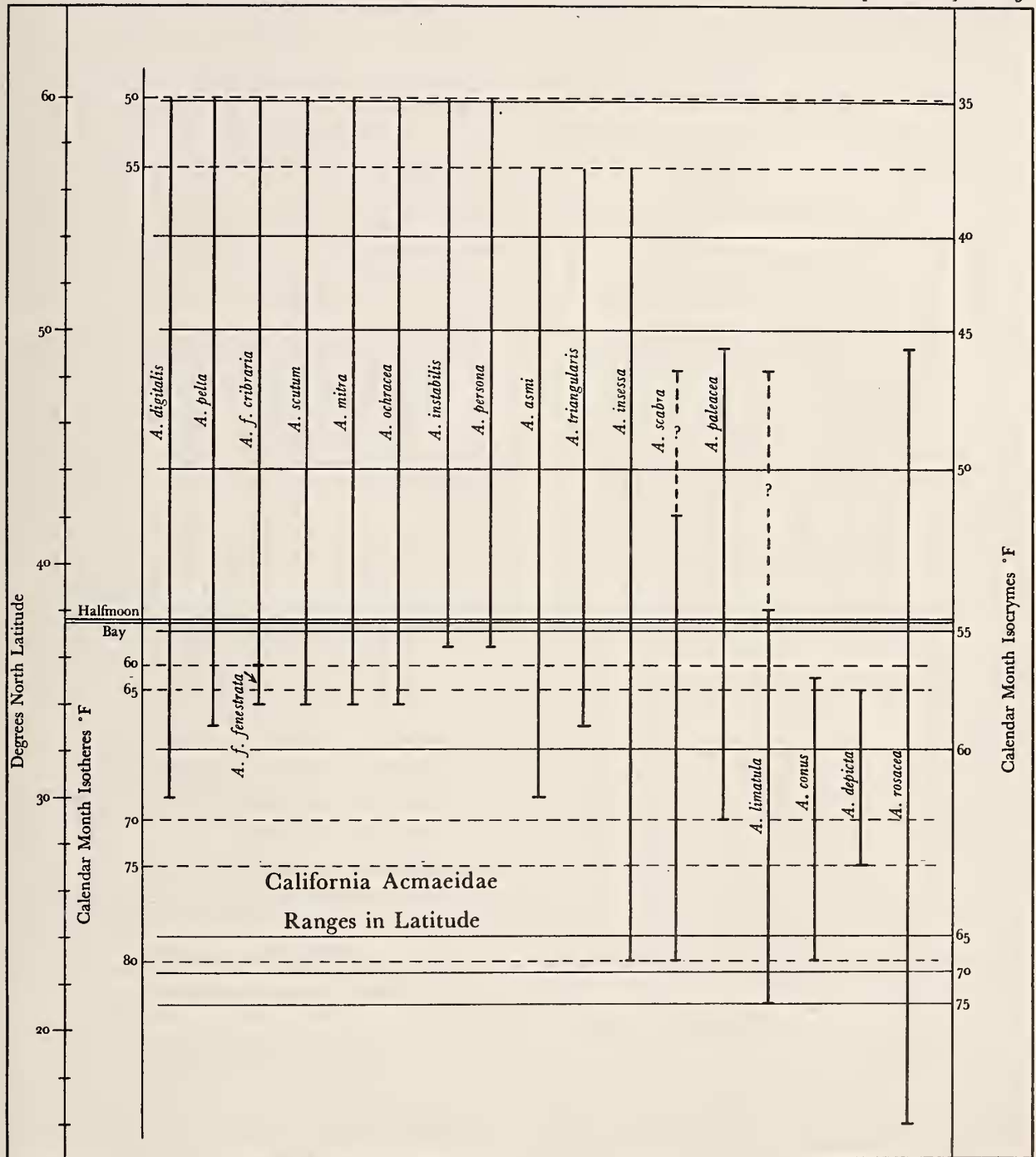
Isocryme range: 35° - 58° F. (23°)

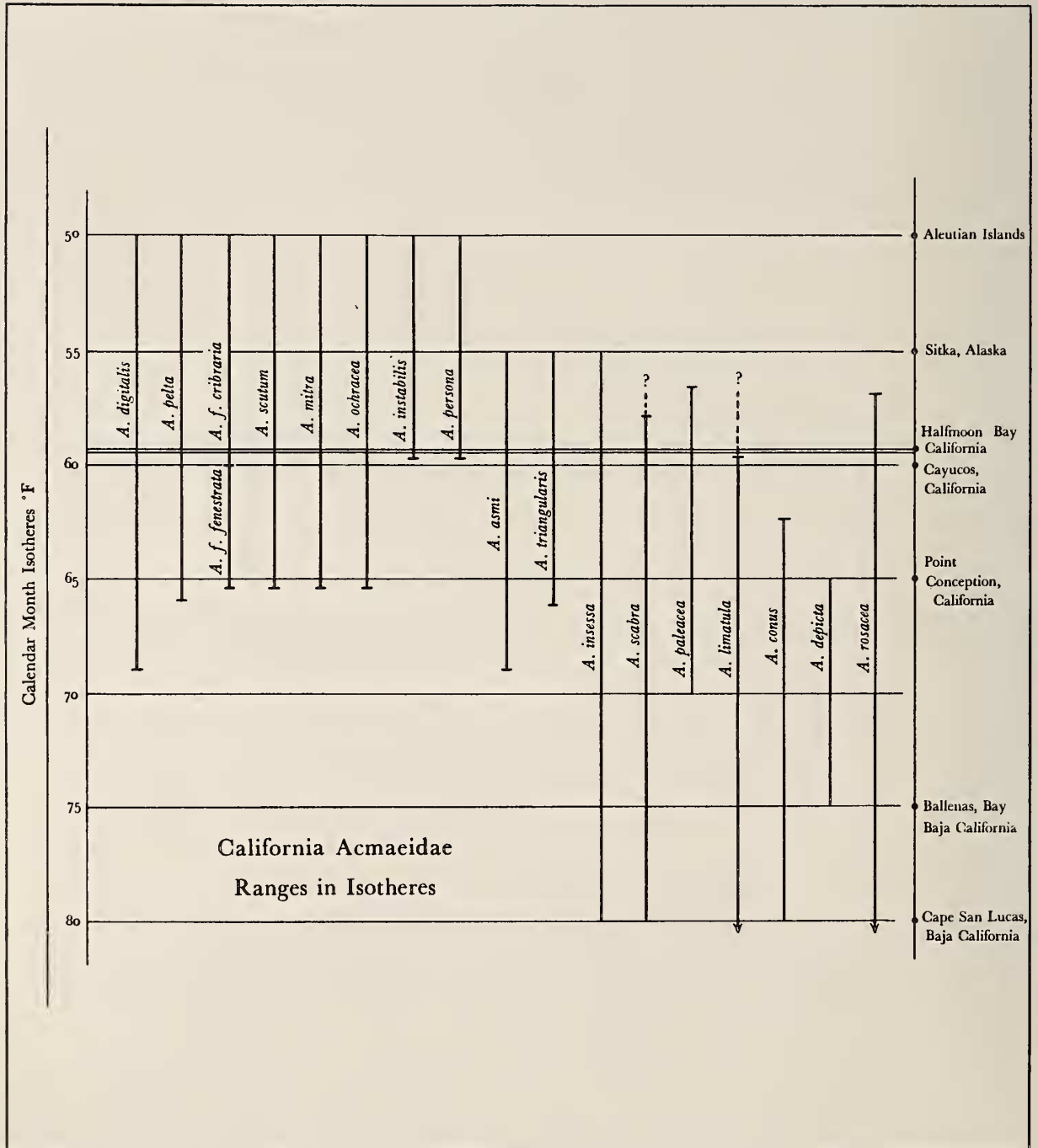
The population of this moderately eurytopic limpet is reproductively active throughout the year (Plate 17, Part II). The gonads redevelop subsequent to each spawning and no sexually indeterminate period is found. There is, however, a tendency toward a summer latent period at which time the gonad is fully developed but spawnings are reduced or stopped. In the absence of data on this species from more southern points, it is difficult to suggest what effect increasing temperature has on its reproduction. Does it, at the southern end of its range, become sexually indeterminate or does it develop gametes without shedding them? Orton (op. cit.) believes that the production of eggs capable of being fertilized is sufficient evidence of breeding activity. Thorson (1946) disagrees with this and points out that in certain regions the temperatures are such that the animals can ripen their gonads but spawning will not occur. As will be shown later, this is presumably the case for two species of Acmaea investigated and may also be true for A. scutum. It is interesting to note that in 1949, 1950, and 1951 the first fall spawning occurred at a time when water temperature was at or very near its maximum. The larvae are thus probably able to survive at sea temperatures near 60° F. and the range of A. scutum in relation to isocrymes substantiates this, since the range of the species terminates at the 58° isocryme.

Acmaea mitra Eschscholtz, 1833

Geographic range: Chirikoff Island, Alaska, to Punta Santo Tomas, Lower California

Latitudinal range: 60° - 31° 35' N. Lat.





Isothere range: 50°-65.5° F. (15.5°)
 Isocryme range: 35°-58° F. (23°)

On Plate 10, Part I, it can be seen that this species is a winter breeder, spawning when the sea temperature is at or near its minimum. The population studied shows a slow redevelopment of the gonads and a fully ripe condition may be reached as early as July, although spawning may not occur until December or January. The maximal temperature at which spawning occurred was in February, 1952, when the surface waters were about 53.5° F. If this value is tentatively taken as the upper limit for spawning and is compared with the isocryme at the southern end of the range (Plate 32), it is seen that the latter figure is approximately 58° F., or 4.5° in excess of the postulated maximal temperature. This discrepancy is probably explained by the fact that *Acmaea mitra* becomes subtidal somewhere on the central or southern California coast and thus may remain in temperature ranges suitable to it.

It is interesting to observe that, in *Acmaea mitra*, the sensitive point in its reproductive physiology is its spawning mechanism and the activity of the gonad seems to be unimpaired unless the slow redevelopment after spawning is so regarded. From the above discussion, it seems certain that *A. mitra* is restricted in its southern distribution by the maximal temperature at which spawning can occur.

Acmaea pelta Eschscholtz, 1833

Geographic range: Aleutian Islands to San Diego, California
 Latitudinal range: 60°-33° N. Lat.
 Isothere range: 50°-66° F. (16°)
 Isocryme range: 35°-59° F. (24°)

This eurytopic species is reproductively active throughout the year and is known to spawn at sea temperatures from 48.5° F. to 60.0° F. (Plate 9, Part III). Furthermore, there is no long summer period during which the gonads are ripe but unspawned as is found in *Acmaea scutum*. This may be related to the slightly greater southern range of *A. pelta*, which itself seems to be uncertain since Keen (1937) lists the species from 19° N. Lat. and Test (1937), while giving San Diego as a southern termination, suggests that it may extend even further.

When a species is reproductively active throughout the year, it is difficult to account for the distribution in terms of temperatures encountered since no critical temperatures have been defined. The best that can be done

with *Acmaea pelta* is to accept tentatively the highest known spawning temperature, 60.0° F., and compare the species range with this particular isocryme. If a relationship is present, the two may be expected to coincide within a few degrees. Plate 32 shows that the range of this species terminates at the 59° F. isocryme, only 1° from the highest determined spawning temperature. It may thus be assumed that *A. pelta*, like other northern species, is restricted to the south by the maximal temperature at which it can spawn. Whether the gonad shows a summer indeterminate phase in the more southern latitudes is not known.

Acmaea digitalis Eschscholtz, 1833

Geographic range: Aleutian Islands to Guadalupe Island, Mexico
 Latitudinal range: 60°-30° N. Lat.
 Isothere range: 50°-69° F. (19°)
 Isocryme range: 35°-61° F. (26°)

Disagreement exists concerning the southern limits of this species which is listed by Keen (1937) as 19° N. Lat. and by Test (1937) as Guadalupe Island, Mexico. Specimens in the collection of the California Academy of Sciences from Guadalupe Island are unmistakably *Acmaea digitalis*, and this is the most southern point from which they have recorded the species. It does not occur on Socorro Island as listed by Dall (1921).

The data on reproduction from the population at Moss Beach (Plate 13, Part III) suggest that the species is active at this latitude throughout the year. The maximum temperature at which spawning occurred was in June-July, 1951, the mean temperature for the period being 56° F. The isocryme for this temperature does not even closely agree with the southern limit of the range, the 56° isocryme falling approximately at 36° N. Lat. or just south of Monterey, California. This continuous breeding is to be expected when the area of study lies near the center of the range of temperature tolerance of a species as is the case for *Acmaea digitalis*.

The data from the Rockaway Breakwater population of *Acmaea digitalis* (Plate 12, Part III) are perhaps more reliable because interpolation, as explained previously, was not necessary to localize spawning periods. The minimum temperature at which spawning occurred was 49.5° F. during February, 1950. This value is approximately the isotherm for the northern limit of the species. Despite the extreme con-

ditions of temperature and desiccation which the breakwater population must endure, there can be no doubt that it is an adequate habitat for the adult limpets. Were this not so, the continual collections which were made there over a period of three years and which totaled more than 9'000 individuals would certainly have drastically reduced the population. This did not happen, and thus the settlement of larvae and their growth must have been continuous. It seems that the extreme environmental conditions affected primarily the activity of the gonads and resulted in the sexually indeterminate summer phase. If it be assumed that this condition is realized throughout the most southern ranges of this species, it is clear that the time of development of the adult gonad restricts breeding times to the period most favorable to the larvae. Presumably the ultimate response of this species, like A. persona, to increasing temperatures would be a nonfunctioning gonad.

Acmaea limatula Carpenter, 1864

Geographic range: Tomales Bay, California, to Tres Marias Islands, Mexico

Latitudinal range: 38° - 21° N. Lat.

The open coast range terminates approximately at Santa Cruz, California, a distribution for which the following temperature ranges are given.

Isothere range: 60° - 80° F. (20°)

Isocryme range: 55° - 75° F. (20°)

This southern species is given a southern limit by Keen (1937) of 24° N. Lat. which is near the southern tip of Lower California. However, Strong and Hanna (1930) found it on the Tres Marias Islands, and the California Academy of Sciences possesses an unmistakable specimen from Socorro Island of the Revillagigedos. The southern range is therefore extended to 21° N. Lat. According to Test (1937) the species is numerous at Pacific Grove, California, but, except for an occasional specimen, is not found north of there or Santa Cruz on the open coast. Pockets of warm water do exist which support the species, one of which is Tomales Bay. Keen (1937) lists the northern limit as Puget Sound, but it is not reported by Curtiss (1941) nor has the author collected it despite extensive collecting there and in the San Juan Islands.

In Tomales Bay the so-called subspecies Acmaea limatula moerchii Dall, 1878, spawns once a year during September at a time when water temperatures are at a maximum of about 60° F. on the open coast (Plate 10, Part III).

This is followed by a period when spawned and sexually indeterminate animals are found and when the gonad is slowly reformed. This cycle correlates well with the distribution of the species, since it terminates just northward of the 60° F. isotherm (Plate 31). It appears that this species is limited in its northward distribution by the temperature required for its spawning. The gonad can redevelop even during the coldest part of the year as shown by the decrease in the numbers of indeterminate animals during the winter months. But, as previously indicated, the gonads of this population do not develop the extreme turgor seen in most of the other species suggesting that the temperatures do not favor maximal reproductive activity.

Acmaea asmi (Middendorf, 1847)

Geographic range: Sitka, Alaska, to San Quintín Bay, Lower California

Latitudinal range: 57° - 30° N. Lat.

Isothere range: 55° - 69° F. (14°)

Isocryme range: 38° - 61° F. (23°)

Acmaea asmi, as would be expected of a species with a southern distribution, is reproductively active during a period from April to September or October and then enters a period of reproductive latency until the following March when gonad redevelopment begins (Plate 11, Part III). The minimum water temperature at which it is known to have spawned at Moss Beach is 52° F. in April, 1951. This figure agrees reasonably well with the 55° F. isotherm which forms the northern limit of the species near Sitka. The reproductive cycle of this species appears to be controlled as much by the effect of low temperature on the gonad as by the requirement for a certain spawning temperature since, unlike A. limatula, its gonad is nonfunctional during the winter months. It would be interesting to know if the animals become sexually indeterminate during the winter in Alaskan waters.

Acmaea scabra (Gould, 1846)

Geographic range: unknown point in Northern California or southern Oregon to Cape San Lucas, Lower California

Latitudinal range: unknown point near 42° to 23° N. Lat.

Isothere range: 58° (California-Oregon border) to 80° F. (22°)

Isocryme range: 50° (California-Oregon border) to 68° F. (18°)

This species is listed by Keen (1937) as

